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Bats of Guana, British Virgin Islands

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ABSTRACT

Three species of bats are newly recorded from Guana Island, north of Tortola: *Artibeus j. jamaicensis, Molossus molossus fortis,* and *Brachyphylla cavernarum* indet. The known range of *B. cavernarum* is extended about 20 km northeastward in the Virgin Islands. Guana, at 297 ha and 266 m, is the smallest island in the Antilles with three species. Island elevation seems more important than area in determining bat species diversity in the Virgin Islands.

INTRODUCTION

Guana Island, in the British Virgin Islands on the greater Puerto Rico Bank, is arid, rugged, and remarkably well forested (Lazell, 1980). It comprises 297 ha and rises to 266 m. Its herpetofauna has been considered in theoretical biogeographic terms (Lazell, 1983a). When that work went to press, eight species of reptiles were known, about twice the number predicted by classic biogeographic theory; since then, several more species have been found. In addition, a tree snail described in 1889, without known geographic provenance, has been rediscovered there (Lazell, 1983b). The island seems unusually rich biotically for its small size.

GUANA BATS

In March 1982, we collected the phyllostomid bats *Artibeus j. jamaicensis* (AMNH 244964–244968) and *Brachyphylla cavernarum* (AMNH 244976) from caves opening at ca. 100 m on the south-facing slope of the island. *Brachyphylla* has been previously recorded for St. John and Norman Island (Koopman, 1975); the Guana record extends the species range 20–25 km farther out on the Puerto Rico Bank (fig. 1). We are unable to recognize the subspecies *intermedia* Swanepoel and Genoways (1978). They divided *B. cavernarum* into three subspecies

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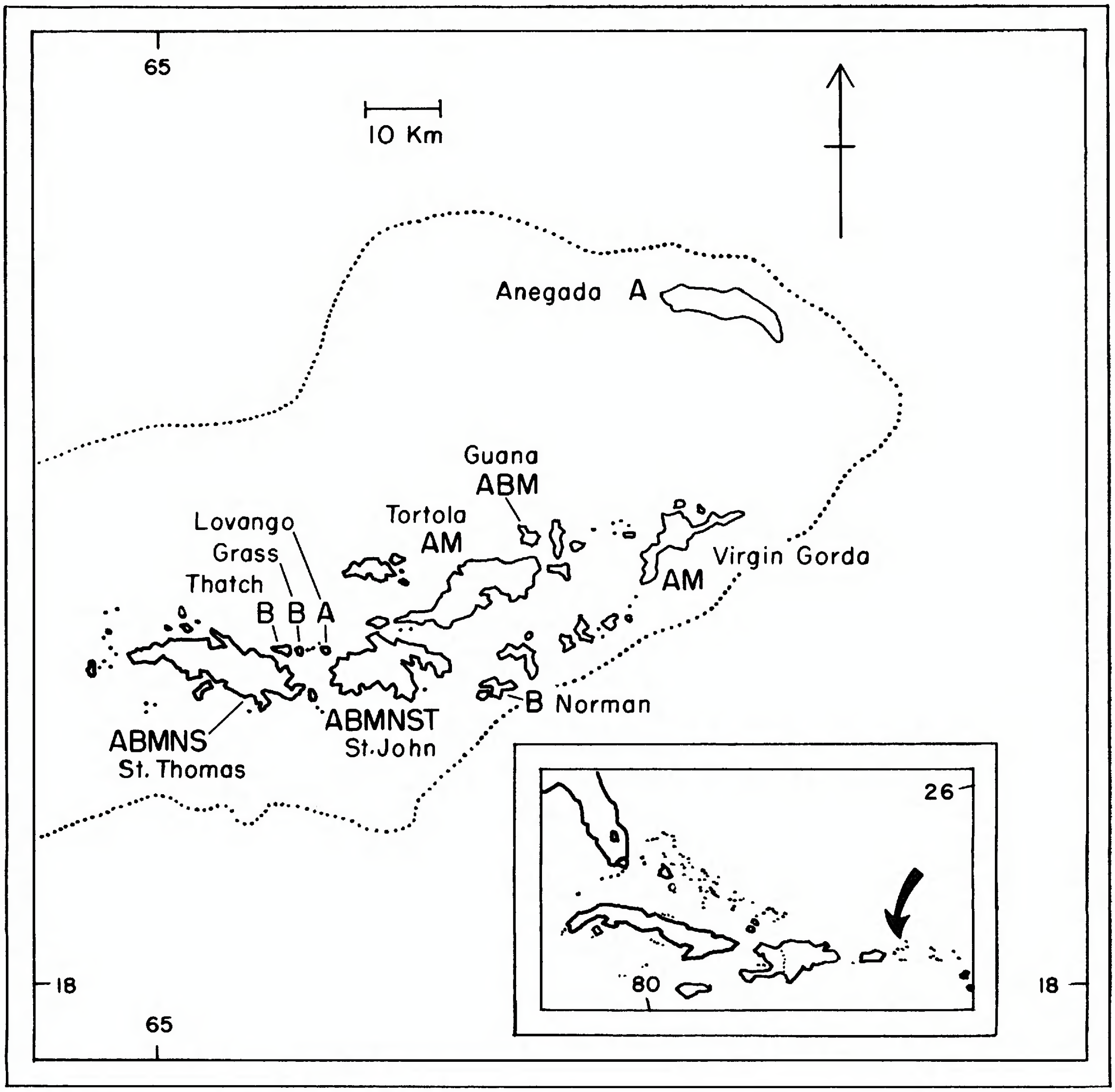

FIG. 1. The Virgin Islands of the greater Puerto Rico Bank, with known bat faunas indicated. A = *Artibeus j. jamaicensis*; B = *Brachyphylla cavernarum*; M = *Molossus molossus fortis*; N = *Noctilio leporinus mastivus*; S = *Stenoderma r. rufum*; T = *Tadarida brasiliensis antillularum*. The dotted line is the approximate limit of land at a glacial maximum. Inset shows the position of the Virgin Islands in the Antilles.

on the basis of size. They classified specimens from St. Croix, southwest of the Anegada Passage, as the purportedly large nominate form, *B. c. cavernarum*, and specimens from the Virgin Islands on the greater Puerto Rico Bank as the smaller, new form, *B. c. intermedia*. Measurements from their table 1 for samples from St. Croix and Puerto Rico Bank Virgins (St. Thomas, St. John, and Norman Island) overlap so greatly as to preclude identification of most individuals to subspecies. For example, forearm length was cited as the most important external measurement. Measurements (in millimeters) are 60.2–65.5 in St. Croix males, 64.5–66.8 in St. Croix females, and "66.5–68.0" in *B. c. intermedia* as a whole (i.e., larger). Our specimen, found mummified and hanging on a cave wall, can-

not be sexed; it has a forearm of 65.9, within the range of Virgin Islands' *intermedia,* given as 60.0–66.4, all males. The Guana specimen is near the mean for St. Croix females of nominate *cavernarum.* We question the utility of recognizing the subspecies *B. c. intermedia* at least until diagnoses can be framed which will permit identification of more individual specimens.

Young of *Artibeus j. jamaicensis* were produced in March 1982 and 1984, and in July 1984. A female, AMNH 244967, contained a large embryo, AMNH 244964, crown–rump length 34 mm, on March 11, 1982. Another female, AMNH 244966, carried her juvenile, AMNH 244965, total length 60 mm and forearm 50 mm, with her in flight when disturbed from her roost on March 18, 1982. A female was mist-netted while carrying her young in flight, March 8, 1984: figure 2 (cf. Fenton and Kunz, 1977, p. 360). Two of four females netted on July 19, 1984, were carrying young measuring 47 and 54 mm, crown–rump length.

On November 6, 1983, Neil Hochstedler captured a female *Molossus molossus fortis* (AMNH 255697) in a building adjacent to an area in which we had frequently observed this species in flight. A pregnant female caught July 8, 1984, contained an embryo 26 mm crown–rump (AMNH 256413); the female had a total length of 110 mm and a forearm of 40 mm (AMNH 256412).

FIG. 2. Adult female *Artibeus j. jamaicensis,* forearm 62 mm, mist-netted in flight carrying her nursing young, forearm 46 mm, on Guana Island, March 8, 1984. Photo by Thomas Jarecki.

OTHER SPECIES

Six species of bats are known from the Virgin Islands (Koopman, 1975). The only island known to support all six is St. John; this, the third largest of the Virgin Islands, is ca. 5180 ha, of which ca. 60 percent is within Virgin Islands National Park. All three of the bats of Guana are present on St. John. A third phyllostomid, *Stenoderma rufum,* is a "rare fruit-eating" species (Koopman, 1975); it may be ecologically restricted to the higher, wetter islands, as Koopman suggested, but all records from the Virgin Islands are from near sea level. The second molossid, *Tadarida brasiliensis,* is known from a single specimen from St. John (Koopman, 1975); this seems inexplicable in view of its penchant for adapting to edificarian habitats and a vast geographic and climatic range. Possibly *Molossus* competitively excludes it. The sixth species is the noctilionid *Noctilio leporinus.* Johnson (1978) provided a sight record of this species from Gorda Sound, Virgin Gorda, and a photograph of one in flight from St. John. *Noctilio* may occur on Guana, but evidence is against it. Many people have reported seeing this very large and distinctive species to one of us (Lazell) around Road Bay on the large island of Tortola. Several people who work around the waterfront at night on Guana agree that they have never seen this animal. Possibly there is insufficient calm water or fresh to brackish water available.

In table 1 we list the islands in the Virgins known to support bats and some characteristics of the bat fauna. *Brachyphylla* live in small sea caves on the little cays of Thatch and Grass, according to William Rainey

TABLE I
Virgin Island Bat Faunas[a]

Island	A	E	*A. jamaicensis*	*B. cavernarum*	*M. molossus*	*N. leporinus*	*S. rufum*	*T. brasiliensis*	I	N	R	S_1	S_2	S_3	S_4	S_5
St. Thomas	7660	470	16	3	5	17	1	—	42	5	4–5	5	6	3	6	5
Tortola	5444	521	6	0	5	S	—	—	11	4	3–4	4	5	4	7	5
St. John	5180	387	72	55	26	3	3	1	160	6	6	4	5	3	5	5
Anegada	3872	9	1	—	0	—	—	—	1	2	1	4	5	0	0	2
Virgin Gorda	2130	414	1	0	1	S	—	—	2	4	1–2	3	4	3	5	4
Guana	297	266	6	2	1	—	—	—	9	3	2–4	2	2	3	3	3
Norman	257	131	—	16	—	—	—	—	16	1	3–4	2	2	2	2	1
Thatch	69	146	—	1	—	—	—	—	1	1	1	1	2	2	2	1
Lovango	45	75	10	—	—	—	—	—	10	1	3–4	1	2	2	1	1
Grass	24	70	—	1	—	—	—	—	1	1	1	1	1	2	1	1

[a] Sample sizes are from Koopman (1975) and material collected or seen by us. A is area in hectares. E is elevation in meters. 0 indicates presumed occurrence, but no specimen. S indicates a sight record not tallied in the sample. I is the total number of individuals in each sample. N is the total number of species per island. The remaining columns to the right give species number predictions based on various theoretical considerations and formulae: R, by rarefaction (Simberloff, 1978), with range of plus or minus one standard deviation; S_1, species: area (MacArthur and Wilson, 1967) using all Virgin Islands data: S_2, the same, but using only four islands: Puerto Rico, St. John, Guana, and Lovango; $S_3 = CE^z$ for all Virgin Islands; S_4, the same using only Puerto Rico, St. John, Guana, and Lovango; S_5, the best-fit formula (Lazell, 1983a) using all Virgin Islands. All numbers are rounded to the nearest whole species. Puerto Rico is about 890,000 ha and 1338 m; it has 16 species of bats (Koopman, 1975).

(Museum of Vertebrate Zoology, Berkeley, personal commun.), who collected the specimens reported by Koopman (1975). These sea caves were cut into Tutu formation sediments of sandstone and limestone by wave action (Sears, in Jarecki, 1983). On Guana, our *Brachyphylla* was from one of numerous caves formed in welded and agglomeratic tuffs by collapse processes resulting from differential reactions to water permeation (Ed Olson, Dept. Geology, Field Museum of Natural History, personal commun.). Koopman (personal commun.) found *Brachyphylla* in a crevice cave roofed by vegetation and humus on St. John.

All three kinds of caves are widespread in the Virgin Islands southwest of Anegada. (Anegada has small solution caves; the island is made largely of oolitic limestone.) Sea caves are present only up to levels reached by Sangamon interglacial seas, a few meters above present sea level. Crevice caves are also best developed where interglacial seas loosened and rolled boulders. Tuff caves can occur much higher, however, to far more than 100 m above present sea level, as on Guana. The presence of these caves may be an important component of an elevation effect rendering higher islands better habitats for a greater diversity of bat species: see table 2.

DIVERSITY AND BIOGEOGRAPHY

We want to know if the bat fauna of Guana is unusual in its diversity (or if other Virgin Islands seem depauperate), what the causal components of bat species diversity seem to be in this archipelago, and what avenues of future investigation might predictably be most worthwhile.

One way of analyzing diversity is by using the statistical technique of rarefaction (Simberloff, 1978). All species:spatial formulations (see below) assume (unstatedly) a rarefaction sequence at some level. We have counted specimens collected throughout the Virgin Islands reported by Koopman (1975), as well as those seen or collected by us. Engstrom and James (1981) and James and Rathbun (1981) apply rarefaction techniques to avian communities which seem a convenient macrocosm of our situation with Guana's bats.

The tallies for all six known bat species in

TABLE 2
Some Components of the Virgin Islands Ecosystem of Importance to Bats and Dependent on Elevation

Elevation[a]	Component	Etiology	Importance
0–15	Sea caves	Wave action: present and interglacial	Roost sites
0–15	Boulder jumbles and crevice caves	Wave action: present and interglacial	Roost sites
0–300	Tuff caves	Differential porosities of welded and agglomeratic tuffs	Roost sites
10–480	Ravine effect	See Lazell (1983a)	Big trees; shelter if hollow, food if fruiting
300–480	Increasing moisture	Reduced temperatures and increasing cloud cover	Tree species not present in lowlands, and therefore of novel feeding potential
>480	Cloud forest	Reduced temperatures and increasing cloud cover	Tree species not present in lowlands, and therefore of novel feeding potential

[a] Approximate; in meters.

the Virgin Islands, arranged in the left-to-right listing of table 1, are 111, 77, 38, 20, 4, 1. The subset for St. John indicates an excellent draw: 72, 55, 26, 3, 3, 1. Using the formula of James and Rathbun (1981), the eight bats collected on Guana should represent two to four species. The three species collected there are the three most common species found on St. John; thus, Guana's bat fauna may be viewed as a subset of St. John's. For the smaller islands, rarefaction methods predicted incorrect numbers of expected species. On Norman and Lovango the number of species expected by rarefaction is three or four, while on both islands only one species is known to be present. In both cases all specimens collected were taken from a single roost site while bats were roosting (Koopman, 1975, and personal commun.); Lovango is both small and low. Expected numbers of species for St. Thomas and Tortola were correctly predicted by the rarefaction formula. If the sample sizes on these islands were increased, the number of species expected would predictably increase also.

In considering species : spatial relationships we used the formula of MacArthur and Wilson (1967). We used all Virgin Islands data available, except for islands on which no bats have been collected ($S = 0$). Then we applied the formula to the four islands we consider to be adequately collected: Puerto Rico, St. John, Guana, and Lovango. Both species:area and species:elevation relationships were approached in this manner.

The species:area equation for all Virgin Islands data is $S = 0.34A^{0.29}$ ($r^2 = 0.756$). This equation for the four best collected islands is $S = 0.58A^{0.25}$ ($r^2 = 0.960$). These formulae predicted less than the actual number of species on St. John and Guana, leading to the conclusion that both islands are biotically rich.

When using elevation (E) instead of area (A), we get the following equation for all Virgin Islands data: $S = 0.38E^{0.35}$ ($r^2 = 0.349$). The formula for species:elevation relationships using only the four best collected islands is $S = 0.017E^{0.95}$ ($r^2 = 0.985$). The latter equation has a high number for the exponent, indicating that elevation is very important in determining the number of species present (Lazell, 1983a). Guana has the predicted number of species for an island of its elevation. Tortola has an especially high number of predicted species; we believe it is presently grossly under collected.

Lazell (1983a) used equations combining area and elevation factors and achieved closest fits to reality with those in planar form.

These equations are not useful over large orders of magnitude in spatial parameters; we cannot include Puerto Rico data here. Using the available Virgin Islands data, $S = C_1A + C_2E + C_3AE - C_4$, with constants: $C_1 = 6.34 \times 10^{-4}$; $C_2 = 9.56 \times 10^{-3}$; $C_3 = -1.21 \times 10^{-6}$; $C_4 = 1.64 \times 10^{-2}$ ($r^2 = 0.934$). Elevation is by far the most important single factor. The predicted S values (table 1) are exact for all islands except St. John and Tortola; the latter has an additional species predicted.

CONCLUSIONS

With three known species, the diversity of bats on Guana is predictable given our sample size (by rarefaction) and the elevation of the island. This diversity is significantly (50%) greater than species:area predictions. Elevation seems to have a great influence on bat species diversity. This relationship is particularly intriguing for the high (and large) island of Tortola, which we predict harbors up to twice the number of species known there at present.

The species:elevation correlation is also intriguing because all known Virgin Island bat species occur in the lowlands. Thus, the greater Puerto Rico Bank seems to provide an insular, oceanic example of the paramontane distribution phenomenon of Koopman (1983).

Apart from Guana, St. John, and Lovango, the Virgin Islands remain insufficiently collected. Where elevation and rarefaction indicate that samples are of a size which should include more species than are known (Norman Island) we suspect single-site roost collecting has introduced bias, and real diversity may be greater.

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